FACTORS AFFECTING NESTING SUCCESS IN GREATER SNOW GEESE: EFFECTS OF HABITAT AND ASSOCIATION WITH SNOWY OWLS

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ABSTRACT.—We examined how habitat features affected nesting success of Greater Snow Geese (*Chen caerulescens atlantica*) on Bylot Island, Northwest Territories, Canada, under high (1993) vs low (1994) nesting success and colonial vs isolated nesting (1994 only). Because Snow Geese nested in association with Snowy Owls (*Nyctea scandiaca*) in 1993, we also examined the relationship between nesting success and distance from owl nests. Predation, especially by Arctic foxes (*Alopex lagopus*), was the main cause of nesting failure on Bylot Island. In 1993, goose nests near an owl nest had better success than those farther away, and they also tended to be initiated earlier. Few habitat features were related to nesting success, although nests located in pond habitat had lower success than those in wet meadows or moist tundra. In 1994, Snowy Owls were absent, and goose nesting success was much lower than in 1993 (23–42% vs 90%). Isolated nests located on hillsides had higher success than those located in lowlands. In contrast, colonial nests were more successful in lowland wet meadows, where tall willow bushes (*Salix lanata*) were present, than in either moist tundra or hillsides. In the latter habitat, nests associated with *Cassiope tetragona,* a plant that typically grows in depressions between hummocks, had higher success than those associated with other vegetation. We conclude that nesting in association with raptors, such as Snowy Owls, that maintain a predator-free area around their nest, was probably a dominant factor affecting Greater Snow Goose nesting success. In the absence of owls, isolated nests had higher success in hilly habitats than in lowlands, whereas colonial nests in tall willows were most successful. *Received 14 Aug. 1996, accepted 25 Feb. 1997.*

Predation often is the dominant factor affecting nesting success in birds and can play a major role in avian population dynamics (Wilcove 1985, Klett et al. 1988). Selection should, therefore, favor birds that use strategies or select sites that minimize the risk of predation. This is especially true in single-brooded species that do not renest after losing a clutch. In some years, nest predation by Arctic foxes (*Alopex lagopus*) causes almost complete breeding failure in tundra-nesting birds such as waders and geese (Summers and Underhill 1987, Anthony et al. 1991, Underhill et al. 1993, Ebbinge and Spaans 1995). Even though species of large body size, such as geese, may sometimes successfully defend their nest against foxes, they nonetheless suffer from predation in years of high fox

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density (Ebbinge and Spaans 1995). Several factors may affect the vulnerability of nests to predation, but one of the most important is nest concealment. Selection of habitats with increased microrelief and vegetation cover should reduce nest visibility and, thus, risk of predation in ground-nesting birds (e.g. Hill 1984, Jackson et al. 1988, Petersen 1990, Schieck and Hannon 1993).

Nesting success can vary considerably among years in arctic-nesting Greater Snow Geese (*Chen caerulescens atlantica*; Lepage et al. 1996). For instance, in 1993, many Snow Geese nested in dense colonies in association with Snowy Owls (*Nyctea scandiaca*) on Bylot Island, and their nesting success was high. In contrast, in 1994, Snowy Owls were absent and the success of geese nesting either in dense colonies or in a more isolated situation was quite low (Lepage et al. 1996). We used this opportunity to examine how habitat features affected nesting success of Greater Snow Geese under these contrasting situations: high (1993) vs low (1994) nesting success and colonial vs isolated situation (1994 only). We hypothesized that habitat features should be more related to nesting success in 1994, a year of low nesting success and of higher predator activity. A second objective was to examine the relationship between nesting success and distance from the owl nest to test the hypothesis that the high nesting success of geese in 1993 was a consequence of their association with Snowy Owls.

METHODS

Study area.—The study took place at the migratory bird sanctuary of Bylot Island, Northwest Territories, Canada. The main study area (73°08′N, 80°00′W) is a large glacial valley (hereafter called the Base-camp valley) bordered by steep hills to the north and southeast and rolling hills to the southwest. The moist upland and lowland tundra there was characterized by plants such as Arctic willow (*Salix arctica*), bell-heather (*Cassiope tetragona*), northern woodrush (*Luzula confusa*), and a sparse graminoid cover. Two wetland types associated with tundra polygons are found in the lowlands: wet meadows with a rich graminoid cover and ponds created by sunken polygons and surrounded by graminoids. In both wetland types, Fisher's dupontia (*Dupontia fisheri*), cottongrass (*Eriophorum* spp.), and water sedge (*Carex aquatilis*) were dominant plant species (Hughes et al. 1994). A secondary study area (72°53′N, 78°55′W), about 30 km south of the base-camp, was also used in 1994 (hereafter called the Camp-2 area). This area was located around a narrow valley about 0.5 km wide and surrounded by low hills with gentle slopes and extensive upland habitats. Hills were dominated by *Salix arctica* and *Cassiope tetragona*, whereas uplands were dominated by *Salix arctica* and some graminoids such as Polar grass (*Arctagrostis latifolia*). Wet meadows were found only in lowlands near the river. Graminoids were abundant in this habitat, and lanate willow (*Salix lanata*), an erect form of willow, was present.

Nesting success.—In the base-camp valley, we found nests during the laying or early incubation period by systematic searches. In the Camp-2 area, nests were found during early incubation. Nests were positioned on a map at ±25 m using a Global Positioning System receiver. A marker was located 10 m from each nest to facilitate locating nests on subsequent

visits. Nests were visited around mid-incubation, at hatch, and after hatch. Number of eggs and signs of predation (total or partial) were recorded at each visit. For nests found after the start of incubation, start of egg laying (laying date) was determined by backdating from hatching date or by estimating incubation stage based on a relationship between egg density and number of days of incubation (Lepage et al. 1996).

Nesting success refers to nests in which at least one egg hatched. We used two methods to estimate nesting success: the traditional method (number of successful nests/number of nests found) and the Mayfield method (Mayfield 1975, Johnson 1979). We present results based on the Mayfield method except in the categorical analyses which require that nests are classified as successful or failed. Results were comparable between the two methods, although the traditional method tended to over-estimate success.

Nest site characterization.—We measured habitat within 30-m of each nest. This distance was chosen because it is the average distance traveled by females from their nest during incubation recesses (Reed et al. 1995). Habitat categories differed slightly between the two study sites and years. In 1993, at the Base-camp valley, habitats were moist tundra, wet meadow, and pond habitat, all located in lowland (no nests were on hillsides). In 1994, because of small sample sizes, only two habitat types were retained in the Base-camp valley—lowland (both wet and moist) and hillside. At the Camp-2 area, habitat types were: lowland wet meadow, hillside and moist tundra. We recorded the dominant vegetation (plant species) within 30-m. In 1993, we scored within 1 m of the nest the presence of microrelief (e.g., frost heaves) or vegetation (e.g., bushes of *Salix lanata*) >15 cm in height from 0% (absent) to 100% (nest completely surrounded) to the nearest 25%. In 1994, we replaced this variable by an index of overall habitat roughness (Rodrigues 1994). Roughness was visually assessed within 30-m of each nest on a scale ranging from 1 to 3. A plot characterized by a large amount of hummocks (humps created by frost action), polygon ridges, and/or rock was rated 3; one with a few hummocks, ridges, or other relief was rated 2; flat terrain with no or little perturbations was rated 1.

Nest locations were plotted on a computer-generated map. From that, we measured the distance between each goose nest and the Snowy Owl nest that was located in the colony in 1993. In both years, nest density was estimated for each goose nest. We defined nest density as the number of nests within a 1-ha circle centered on each nest (minimum nest density according to this method was thus 1 nest ha^{-1}).

Data analysis.—We used logistic analyses to evaluate simultaneously the effect of several variables and their interactions on nesting success. These analyses treated nesting success as a binary response variable (1 = successful, 0 = failed). In 1994, an arbitrary value (0.1) was added to all cells of the contingency table to solve empty cells problem (SAS Institute Inc. 1988). We first built a general model with all variables and their interactions. Interactions were then deleted, one at a time, from higher to lower levels, until only significant interactions remained (Christensen 1990). This procedure was repeated until we reached the simplest model which still fitted the data. At each step, the reduced model was compared with the previous model with a likelihood-ratio χ^2 test (SAS Institute Inc. 1988). These analyses were performed with the CATMOD procedure of SAS.

Comparisons of Mayfield nesting success estimates were made by applying z-tests on the daily mortality probabilities as suggested by Johnson (1979). Because this procedure is a series of pairwise comparisons among different categories of a variable, the Bonferroni correction was used to adjust the significance level (0.05/c where c is the number of pairwise comparisons for the study variable). α values after the Bonferroni adjustment are reported for each comparison.

We examined whether laying date and clutch size were related to distance from the Snowy Owl nest and nest density with linear regression. The effect of habitat on laying date and

clutch size was tested with an ANOVA or Kruskal-Wallis test if distribution departed from normality.

RESULTS

Causes of nest failure.—Several lines of evidence suggest that predation was the main cause of nest failure for geese on Bylot Island. First, abandoned clutches were rarely found despite frequent nest visits (only 2% of failed nests contained intact, abandoned clutches; N = 124 nests). All other nest failures occurred after all the eggs disappeared or were broken. A nest failure often occurred after partial predation, i.e. disappearance of some eggs (in 57% of nests with a visit <5 days before the failure; N = 82 nests). Second, attacks on goose nests by predators were frequently observed in all years that goose nesting activity was monitored on Bylot Island (1989–1994, except in 1993; see below). The Arctic fox was most often observed attacking goose nests. Other nest predators included the Parasitic Jaeger (*Stercorarius parasiticus*), Long-tailed Jaeger (*S. longicaudus*), Glaucous Gull (*Larus hyperboreus*), and Common Raven (*Corvus corax*).

Fox activity at the goose colonies appeared to be very different between the two years. Even though three active fox dens were found within 6 km of the goose colony in 1993, we never observed a fox in the colony during our regular nest checks. In contrast, fox activity at the goose colony was constant in 1994. We witnessed several successful attacks by foxes on goose nests at all our visits to the colony, and at least four different foxes were observed at the same time in restricted areas of the Camp-2 colony (based on variation in fur coloration).

Factors affecting nesting success in 1993.—In 1993, the only Snow Goose colony found in the Base-camp valley was located in the lowlands. Nests (N = 236) were concentrated over a 1.5-km^2 area around a Snowy Owl nest, forming a dense colony ($\bar{x}$ = 3.9 ± 0.22 [SE] nests ha^{-1}). The arithmetic center of the colony was located only 66 m from the owl nest. Overall nesting success was 89.8 ± 2.2%.

We first included all nest site variables and their interactions in the logistic analysis. However, interpretation of this general model was difficult because most of the interactions were not calculated due to missing combinations of variables. We thus preferred a reduced model (Table 1) which excluded two variables which were not significant in the general model (dominant vegetation, microrelief around the nest, and their interactions) even though it did not fit the data as well (χ^2 = 39.5, df = 25, P = 0.03). This analysis revealed that nesting success varied according to habitat type and decreased with increasing distance from the Snowy Owl nest (Table 1). However, significant interactions among variables

TABLE 1

LOGISTIC ANALYSIS OF NESTING SUCCESS IN RELATION TO HABITAT, DISTANCE FROM SNOWY
OWL NEST (DISTANCE), AND NEST DENSITY AT THE SNOW GOOSE COLONY OF THE BASE-
CAMP VALLEY IN 1993

Variables	df	χ^2	P
Habitat	2	6.12	0.01
Distance	1	5.02	0.03
Density	1	2.79	0.09
Habitat × distance	1	—	—[a]
Habitat × density	2	2.66	0.10
Distance × density	1	3.93	0.05
Habitat × distance × density	2	3.92	0.05

[a] Interaction not calculated due to missing categories of habitat and density. Model fit: $\chi^2 = 80.8$, df = 199, $P = 0.99$.

suggested that the effect of distance from the owl nest may vary with
nest density and also among habitats.

Pairwise comparisons showed a higher nesting success (Mayfield es-
timate) in pond habitat (59%) than in wet meadow (93%, $P < 0.02$) and
moist tundra (95%, $P < 0.02$) and a trend for lower success with increas-
ing distance from the owl nest (95% for nests <200 m from the owl vs
87% for nests >400 m, $P > 0.05$). However, these comparisons may be
affected by the interaction between habitat and distance from the owl nest
because habitats were distributed unevenly within the colony, with pond
habitat occurring mostly at the periphery of the colony. To control for
that, comparisons among habitats were repeated using only nests located
in the range of distance from the owl where the three habitats were rep-
resented. Differences among habitats were similar (Table 2), although no
longer significant ($P > 0.14$), possibly because of small sample size. The
effects of distance from the owl nest and density were also examined,
excluding pond habitat, and both factors were again not significant (Table
2). However, pairwise comparisons are less powerful because, unlike the
logistic analysis, they treat distance as a categorical variable, thus losing
information.

We examined the effect of the previous variables on other components
of reproduction. We found a weak but significant relationship between
laying date and distance from the Snowy Owl nest as early-nesting geese
tended to settle closer to the owl nest than late nesting ones (Fig. 1).
Based on the number and size of young hatched in the owl nest in early
July, we estimated that it was initiated around 20 May, 10 days earlier
than the first goose nest (assuming a laying rate of one egg every other
day and a 32-day incubation period starting on the day the first egg is

TABLE 2

MAYFIELD NESTING SUCCESS (%) OF SNOW GOOSE NESTS ACCORDING TO HABITAT, DISTANCE FROM SNOWY OWL NEST, AND DENSITY AT THE COLONY OF THE BASE-CAMP VALLEY IN 1993

Variables	N	Nesting success	
		$\bar{x}$	SE
Habitat[a]			
Pond	15	58.8 A[b]	15.8
Wet meadow	23	88.2 A	7.8
Moist tundra	21	100.0 A	0
Distance to owl nest[c]			
0–200 m	70	95.0 A	2.8
200–400 m	73	93.6 A	3.0
400–1000 m	56	92.8 A	4.0
Nest density			
1–2 nests ha^{-1}	82	95.2 A	2.7
3–5 nests ha^{-1}	58	92.0 A	3.8
6–14 nests ha^{-1}	60	94.2 A	3.2

[a] This analysis was restricted to nests in the range of distance (445–890 m) from the owl where all three habitats were represented because of the significant interaction between habitat, nest density and distance from the owl nest (see Table 1).

[b] Means with the same letter do not differ significantly ($\alpha = 0.02$) within each variable.

[c] Nests from the pond habitat were excluded because of the significant interaction between habitat, nest density, and distance from the owl nest (see Table 1).

laid in Snow Owls; Parmelee 1992). We also found a weak inverse relationship between laying date and nest density ($r^2 = 0.03$, $P = 0.03$, N = 236). However, this observation may not be entirely independent from distance to the Snowy Owl nest as suggested by the correlation between distance and density (Spearman $r = -0.69$, $P < 0.001$). There was no difference in laying date among habitats (ANOVA; $P = 0.86$). Clutch size was not related to distance from the Snowy Owl nest ($P = 0.44$) nor to nest density ($P = 0.52$) and did not differ among habitats (Kruskal-Wallis; $P = 0.56$).

Factors affecting nesting success in 1994.—In 1994, we found only 51 nests in the Base-camp valley. Most of these nests were isolated and scattered throughout the study area (mean density: 1.08 ± 0.04 nests ha^{-1}), and their success was very low ($\bar{x} = 23.1 ± 6.9\%$). At the onset of incubation, a large goose colony (>2000 nests) was found 30 km south of the base-camp (Camp-2 area). A sample of nests (N = 269) was monitored at this colony. Density was high ($\bar{x} = 6.80 ± 0.20$ nests ha^{-1}), but success also was low ($\bar{x} = 42.0 ± 3.6\%$). No owls were found nesting in either study area in 1994. Snow melt was early in both 1993 and 1994,
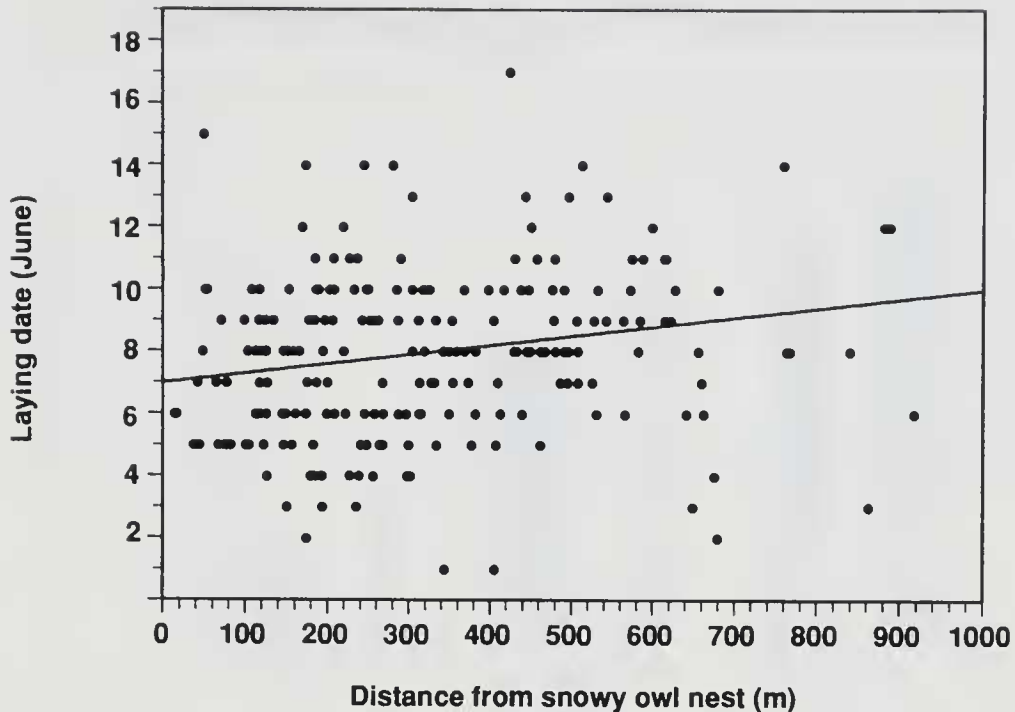
FIG. 1. Snow Goose egg laying date in relation to distance from the Snowy Owl nest at the colony of the Base-camp valley in 1993. $Y = 3.0E - 3X + 156.0$, $r^2 = 0.04$, $P = 0.005$ (in the regressions, X is expressed in Julian date).

and thus the effect of snow cover on nest site availability was probably minimal in both years.

Logistic analysis was not done for the Base-camp valley in 1994 because of small sample size. Pairwise comparisons of the Mayfield nesting success revealed that hillside nests had much higher success than lowland nests ($\bar{x} = 40.1 \pm 10.3\%$, N = 33, vs $1.5 \pm 2.2\%$, N = 14; $P < 0.05$). Nesting success did not vary among different categories of vegetation or habitat roughness around the nest.

At Camp-2 colony, we first built a general model with all the variables and their interactions, using the logistic analysis. A reduced model, excluding all non-significant interactions, fitted the data as well ($\chi^2 = 28.5$, df = 57, $P = 0.99$) and was thus retained (Table 3). This analysis revealed that habitat roughness significantly affected nesting success, whereas the effect of habitat approached significance ($P = 0.07$), but vegetation and density had no effect (Table 3). However, there was a strong interaction between habitat and the dominant vegetation. Pairwise comparisons of the Mayfield nesting success showed that success was lower in medium roughness habitats than in low or high roughness, but sample size in low roughness habitats was low (N = 8; Table 4). Nesting success was higher in wet meadows than on hillsides and moist tundra, and nests located in

TABLE 3

LOGISTIC ANALYSIS OF NESTING SUCCESS IN RELATION TO HABITAT, DOMINANT VEGETATION, HABITAT ROUGHNESS, AND NEST DENSITY AT THE SNOW GOOSE COLONY OF THE CAMP-2 AREA IN 1994[a]

Variables	df	χ^2	P
Habitat	2	5.45	0.07
Vegetation	3	1.30	0.73
Roughness	2	6.25	0.04
Density	1	1.86	0.17
Habitat × vegetation	6	18.74	0.005

[a] Model fit: χ^2 = 29.1, df = 58, P = 0.99.

TABLE 4

MAYFIELD NESTING SUCCESS (%) OF SNOW GOOSE NESTS ACCORDING TO HABITAT, DOMINANT VEGETATION, HABITAT ROUGHNESS, AND NEST DENSITY AT THE COLONY OF THE CAMP-2 AREA IN 1994

Variables	N	Nesting success	
		$\bar{x}$	SE
Habitat			
Hillside	71	29.8 A[a] [b]	6.0
Moist tundra	176	45.8 A	4.4
Wet meadow	22	85.0 B	9.8
Vegetation			
Salix arctica	96	31.8 A[c]	5.4
Cassiope tetragona	105	45.0 A	5.8
Salix lanata	10	100.0 B	0.0
Others	58	35.8 A	7.1
Roughness			
Low	8	78.2 A[b]	19.4
Medium	142	33.5 B	4.5
High	119	51.1 A	5.6
Density			
1–5 nests ha^{-1}	121	48.5 A[d]	5.5
6–20 nests ha^{-1}	146	37.3 A	4.7

[a] Means with the same letter do not differ significantly within each variable.
[b] α = 0.02.
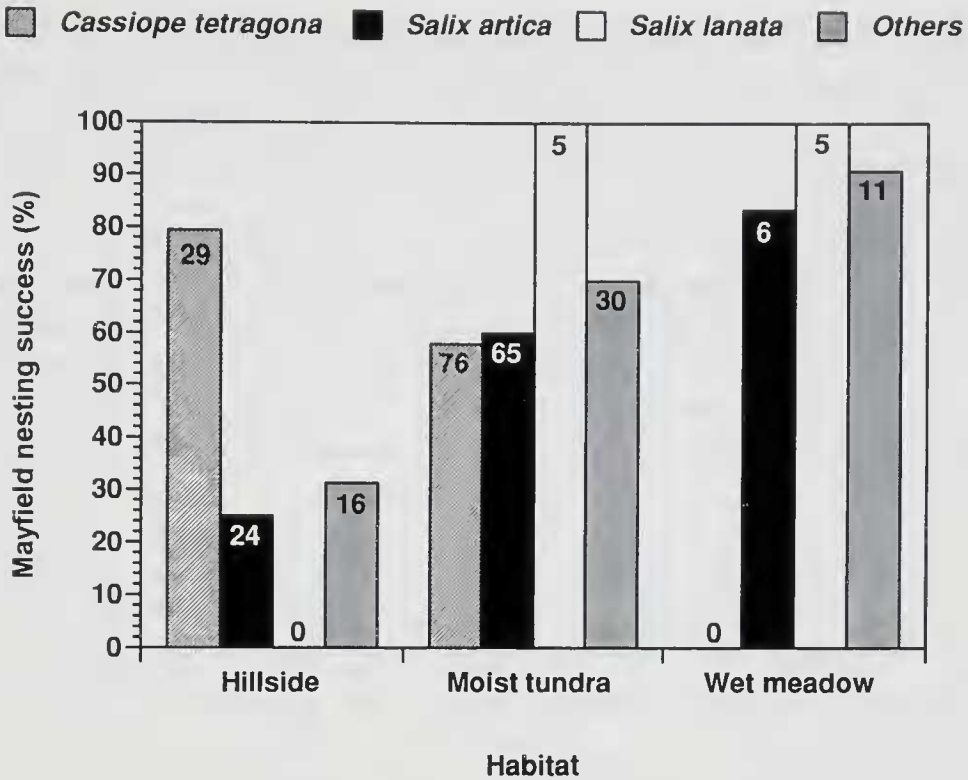[c] α = 0.008.
[d] α = 0.05.

FIG. 2. Mayfield nesting success according to habitat and dominant vegetation at the Snow Goose colony of the Camp-2 area in 1994. Numbers inside the bars are sample size (a zero indicates that no nests were found in this combination of habitat and vegetation).

Salix lanata were more successful than those associated with other vegetation (Table 4). The source of the habitat × vegetation interaction appeared to be the high success of nests associated with *Cassiope tetragona* compared with those associated with other plant species in the hillside habitat but not in the moist habitat (Fig. 2).

In contrast to 1993, we found no relationship between laying date and nest density in 1994 (Camp-2 colony only) nor between clutch size and nest density (all $P > 0.1$). Laying date did not differ among habitats (Kruskal-Wallis; $P = 0.92$), although clutch size tended to be higher in wet meadow ($\bar{x} = 4.1 \pm 0.2$) than in the two other habitat types (hillside: 3.4 ± 0.1, upland: 3.6 ± 0.1; $P = 0.07$).

DISCUSSION

Association with Snowy Owl.—Lepage et al. (1996) suggested that the high nesting success of geese in 1993 compared to other years, and especially 1994, was related to their nesting association with Snowy Owls. The decrease in nesting success with increasing distance from the owl nest in 1993 further supports this hypothesis. Although this effect may be confounded by a density effect (i.e., nest density was higher near the

owl nest), the absence of nest density effect in 1994 suggests that distance from the owl was the dominant factor in 1993. It is also interesting to note that the few nests clustered around a Rough-legged Hawk (*Buteo lagopus*) nest in 1994 had a high success compared to the other nests that year (Lepage et al. 1996).

Nesting associations with Snowy Owls and Rough-legged Hawks have been reported for Snow Geese on Jenny Lind Island, Canada, and Wrangel Island, Russia, and for Brant (*Branta bernicla*) on Taimyr Peninsula, Russia (Parmelee et al. 1967, Litvin et al. 1985, Dorogoi 1990, Syroechkovskiy et al. 1991, Summers et al. 1994). This suggests that nesting in association with raptors is a strategy used by some geese to increase their nesting success. Association of geese with owls was widespread on Bylot Island in 1993 (Lepage et al. 1996). The first geese to settle at the colony also tended to be closer to the owl nest which was initiated before the geese arrived. Nesting near owl nests can be an effective anti-predator strategy for geese because owls chase off predators such as foxes, thus maintaining a predator-free area around their nests. One of us (JPT) observed an owl attacking an Arctic wolf (*Canis lupus*) 750 m from its nest and successfully chasing it. Parmelee (1992:8) reported about Snowy Owls that "Individuals will attack almost anything they consider threatening to their eggs or young, up to 1 km from their nest". This agrees well with our observations that goose nesting success remained high up to several hundred meters from the owl nest (see also Summers et al. 1994). Nesting near owls entails little cost for geese because owls rarely prey on goslings (Lepage et al. 1996).

Nesting by Snowy Owls is uncommon in our study area (Lepage et al. 1996). Nesting propensity of Snowy Owls is strongly dependent on the abundance of their main prey, lemmings (*Lemmus sibiricus* and *Dicrostonyx groenlandicus*), which undergo large cyclic fluctuations (Larson 1960, Summers and Underhill 1987, Syroechkovskiy et al. 1991, Parmelee 1992, Underhill et al. 1993). Massive reproduction of owls (Lepage et al. 1996) as well as foxes, combined with our direct observations of numerous lemmings, suggest that 1993 was a peak in lemming abundance on Bylot Island. Low nesting success of geese in the following year may have been exacerbated by high abundance of foxes following their good breeding performance in the peak lemming year, and the low abundance of lemmings, the main prey of foxes, as suggested by Underhill et al. (1993) in Brant.

Low predation rates on bird nests in years of lemming abundance has been attributed to prey switching by foxes which then concentrate their foraging effort on lemmings rather than eggs (Larson 1960, Summers 1986, Dhondt 1987, Syroechkovskiy et al. 1991, Underhill et al. 1993).

However, our results suggest that association with owls could be another important factor involved in the high nesting success of some arctic birds in years of lemming abundance.

Habitat effects.—As anticipated, few habitat-related features were associated with goose nesting success in 1993. The high success resulting from the association with Snowy Owls probably obscured most habitat effects. The low success in pond habitat may be confounded by the owl effect, because all nests located in this habitat were at the periphery of the colony, far from the owl nest. However, it is also possible that the open structure of pond habitat increases the vulnerability of nests to predation. In this habitat, nests are located on the elevated rims of polygons which may provide easy travel corridors for foxes and reduce the area that needs to be searched.

The situation was different in 1994, as any habitat-related feature that may have reduced the risk of nest predation was probably important. In the Base-camp valley, predation pressure by foxes was intense, especially for lowland nesting geese. Isolated nests located on the hills appeared to be the most successful strategy of geese under these circumstances. The rugged terrain of hillsides may have enhanced concealment of isolated nests or, alternatively, foxes may prefer to hunt in the lowlands.

When nesting colonially at Camp-2, geese were more successful in wet meadows than on hillsides and moist tundra. This suggests that high nesting density may increase the vulnerability of nests in hillsides in contrast to isolated nests. Differences in vegetation characteristics of wet meadows between the two study areas could also have contributed to high success of nests in this habitat at Camp-2. Meadows in the Camp-2 area were restricted to a narrow band near the river where *Salix lanata* bushes were abundant. All nests located in *Salix lanata,* the only plant in our study area that grows high enough (up to 50 cm) to form bushes which can effectively conceal an incubating goose, were successful. However, abundance of this vegetation in the meadows along the river also may have enhanced concealment of nests not directly associated with this plant by limiting ability of foxes to detect nests from long distances in this habitat. This may also explain the higher clutch size of nests found in meadow habitat, as better concealment probably resulted in a lower rate of partial predation. The importance of tall willows in protecting goose nests from predation has also been reported by Jackson et al. (1988) for Lesser Snow Geese (*Chen caerulescens caerulescens*) nesting along Hudson Bay. However, the very restricted distribution of *Salix lanata* on Bylot Island limits its availability as protective cover for nesting geese there.

Increased nest concealment in hummock depressions along slopes may also account for the higher success of nests associated with *Cassiope*

tetragona in hillside habitats. *Cassiope* typically grows in depressions between hummocks that are often >15 cm deep, especially on hillsides, and it is the only regular microrelief that conceals a goose nest on the tundra. Therefore, both micro-habitat features as well as the general landscape or habitat may affect the vulnerability of nests to predation.

In conclusion, association with Snowy Owls had an overriding effect on nesting success in Greater Snow Geese, although this conclusion is largely based on detailed observations at one owl nest. In the absence of owls, both habitat and nest dispersion influenced nesting success, but their effects were variable, possibly due to variation in predation pressure.

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